Responses of marine phytoplankton communities to environmental changes: new insights from a niche classification scheme

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Abstract

Predicting changes of phytoplankton communities in response to global warming is one of the challenges of ecological forecasting. One of the constraints is the paucity of general principles applicable to community ecology. Based on a synecological analysis of a decadal-scale database, we created a niche habitat classification scheme relating nine phytoplankton groups to fifteen statistically refined realized niches comprised of three niche dimensions: temperature, irradiance, and nitrate concentrations. The niche scheme assigned the nine phytoplankton groups to three types of niches: a cold type, a warm type, and a type associated with high irradiance and high nitrate concentrations. The fact that phytoplankton groups in cold niches were governed by irradiance and those in warm niches by nitrate is consistent with general ecological theories, but the fact that diatoms were the only dominant group in high-irradiance, high-nitrate niches challenges the idea based on autecological studies that diatoms are generally better adapted to low-irradiance, high-nutrient conditions. When combined with an irradiance model, the niche scheme revealed that photoinhibition of *Prochlorococcus*, which is predicted from autecological studies, is a function of temperature. We used the niche scheme to predict the responses of phytoplankton communities to environmental changes due to seawater warming and eutrophication. The results of the study suggest that a synecological analysis of large databases from field studies facilitates identification of general principles of community ecology that can be used to forecast responses of biological communities

to environmental changes.

Keywords: Phytoplankton community; climate change; synecology; niche classification scheme; South China Sea.

1. Introduction

Whether general ecological principles will emerge from studies of community ecology is a question that has been debated for at least several decades (Eppley 1972, Lawton 1999), but especially after the concept of a *periodic table of niches*, analogous to the periodic table of elements, was proposed by Pianka (1974). The desire to generate such general theories has been stimulated by concerns over the impact of climate change on biological communities (Mcgill et al. 2006). Winemiller et al. (2015) state that "A universal periodic table of niches is unlikely, but instead alternative niche schemes could be developed for making predictions for different groups of organisms in different regions, or for addressing different kinds of problems." They have proposed feasible methods for creating niche schemes from a functional traits perspective as opposed to pairwise species interactions with no environmental context (Winemiller et al. 2015). They suggest use of a niche scheme that involves 1440 possible niches consisting of five niche dimensions, including habitat (4 levels), life history (5 levels), trophic position (6 levels), defense (2 levels), and metabolism (6 levels). However, it is doubtful that a niche scheme based on so many possibilities is going to be of much practical use. So many niches violate a general principle of science, Occam's Razor, which argues that the number of entities

(e.g., niches) should not to be multiplied beyond necessity (Baker 2007).

In practical applications, the choice of niche dimensions is very much a function of the anticipated application of the niche scheme. To develop a niche scheme that can be used to predict the response of a biological community to climate change, it seems reasonable to begin by using habitat as the niche dimension and ignore the other four dimensions mentioned by Winemiller et al. (2015). The reason is that it is primarily the habitat that we believe climate change will affect, and the distribution of habitats in the future may, in many cases, amount to a rearrangement of habitats in the contemporary environment (Irwin et al. 2012). If the habitats associated with a large-scale field study are sufficiently comprehensive, it may be possible to define a niche table and associated ecological communities that would make possible an informed assessment of the impact of climate change on the composition of communities if future habitats can be characterized with sufficient accuracy.

Predicting future changes from niche schemes is of fundamental importance in the case of marine phytoplankton, which are essential components of most marine biogeochemical cycles and food webs (Falkowski et al. 1998) and are likely to undergo significant changes in terms of biomass, community structure, and diversity in response to sea surface warming and ocean acidification (Barton et al. 2010, Boyce et al. 2010, Follows et al. 2007, Gao et al. 2012). However, phytoplankton as a whole are evolutionarily and ecologically diverse and include tens of thousands of species (Sournia et al. 1991). Assigning all species to a variety of niches based on

64 autecological information would be very challenging, and tests conducted with
65 several species or functional types may not adequately represent natural
66 phytoplankton communities (Mutshinda et al. 2017). Hence there is still much
67 uncertainty about the extent to which the impacts of climate change on natural
68 phytoplankton communities can be generalized from autecological studies. An
69 informed assessment of the likely impact of climate change on phytoplankton
70 communities is more likely to result from a synecological study that identifies
71 practical niche schemes in which information about whole phytoplankton
72 communities can be the basis of niche assignments.

73 One approach to developing such niche schemes based on synecological
74 information is to use simplified indicators to characterize phytoplankton community
75 composition. Phytoplankton community composition estimated from CHEMTAX on
76 the basis of specific marker pigments is one such indicator (Mackey et al. 1996).
77 CHEMTAX is remarkable for its ability to characterize the whole phytoplankton
78 community from picoplankton to large colonies at one time (Mackey et al. 1996).
79 Although the information is limited to taxonomic characterizations at the class level,
80 its advantage is that it facilitates analysis of large datasets.

81 To create a niche scheme that is useful for predicting phytoplankton community
82 responses to climate change, we used a large-scale field dataset collected from the
83 South China Sea (SCS), the largest marginal sea in the Western Pacific. The dataset
84 contained the full size range of phytoplankton communities estimated from

CHEMTAX and covered a wide range of environmental conditions that characterize their habitats. Biogeographic distribution patterns of phytoplankton based on this dataset have been published previously (Xiao et al. 2018b), but there has been no prognosticative analysis of the impact of climate change on the SCS phytoplankton communities. Here, we systematically interpolated the data and developed a niche scheme relating phytoplankton communities to changes of three habitat-related niche dimensions: temperature, irradiance, and nitrate concentrations. Our goal was to predict the response of the composition of phytoplankton communities to future environmental changes using the niche classification scheme.

2. Materials and methods

2.1. Data sources

We previously compiled a dataset based on 5338 samples that were analyzed for phytoplankton community composition and associated environmental parameters. The samples were collected during 20 cruises in the SCS conducted from February 2004 to July 2015 (Chen et al. 2014, Chen et al. 2011, Han et al. 2012, Huang et al. 2010, Wang et al. 2016, Wang et al. 2018, Wang et al. 2015, Xiao et al. 2018b, Yang et al. 2015, Zeng et al. 2015). The relative contributions of nine phytoplankton groups to the total chlorophyll *a* (TChl *a*, the sum of monovinyl chlorophyll *a* and divinyl chlorophyll *a*) were calculated using the CHEMTAX program based on thirteen diagnostic pigments that were determined by high-performance liquid

chromatography (HPLC) (for details, see Xiao et al., 2018b). The nine phytoplankton groups included dinoflagellates (Dino), diatoms (Diat), haptophytes_8 (Hapt_8), haptophytes_6 (Hapt_6), chlorophytes (Chlo), cryptophytes (Cryp), *Prochlorococcus* (Proc), *Synechococcus* (Syne), and prasinophytes (Pras).

For the present analysis, we excluded the coastal region where the bottom depth was less than 50 m because the nutrient sources and hydrological conditions in the coastal region are complex (Han et al. 2012) and the irradiance data are less reliable (Lee et al. 2007). We focused on the dynamics of phytoplankton communities in the upper mixed layer, where global warming effects are likely to be greatest (Six et al. 2007). Similar to other regions worldwide (Johnson et al. 2006, Karl and Church 2014, Laws 2013), high cell abundance, biomass, and relative abundances (contributions to TChl *a*) of most of the dominant groups were generally highest in the upper mixed layer in our study area (Fig. S1).

Among the environmental factors that define niche dimensions, we focused on temperature (°C), irradiance at depth (mol quanta m^{-2} d^{-1}), and nitrate concentrations (μmol L^{-1}) because these factors have been demonstrated to be the most important determinants of phytoplankton community structure in the SCS (Ho et al. 2015, Xiao et al. 2018b). Xiao et al. (2018b) have described details of the acquisition and quality control of these parameters. Because the present analysis focused on the upper mixed layer, the relative abundance of each group and the values of each environmental factor were averaged over the mixed layer by trapezoidal integration with the

126 exception of the mean irradiance in the euphotic zone ($\bar{E}$), which was computed as
127 follows:

128 $$\frac{1}{MLD}\int_0^{MLD} E_0 e^{-k_d z}\, dz = \frac{E_0}{k_d MLD}(1 - e^{-k_d MLD}) \quad (1)$$

129 where

130 $$k_d = \ln(0.01)/Z_e \quad (2)$$

131 where z is the integration variable representing depth (m) in the mixed layer, *MLD* is
132 the mixed layer depth, and k_d is the light attenuation coefficient. Z_e is the depth of the
133 euphotic zone, calculated according to Lee et al. (2007); E_0 is the monthly surface
134 photosynthetically active radiation (400–700 nm) obtained from the standard
135 MODIS-Aqua Level-3 products at 9 km-pixel resolution
136 (http://oceandata.sci.gsfc.nasa.gov/MODISA).

137 After being averaged over the mixed layer, the total number of samples was 689,
138 among which 140 samples had no nitrate data. The result is that we had 549 samples
139 in all analyses if nitrate was incorporated.

140 *2.2. Data interpolation for individual niche schemes*

141 The mean temperature, mean irradiance, and mean nitrate in the mixed layer
142 were in the ranges of 20.6–31.2 °C, 1.9–47.4 mol quanta m^{-2} d^{-1}, and 0.001–8.6 μmol
143 L^{-1}, respectively. To investigate the succession of phytoplankton communities along
144 each niche dimension in the mixed layer, we assigned each sample to different

145 intervals of each niche dimension. The number of intervals was 1 greater than the
146 number of boundaries because the first and last interval included all values less than
147 the lowest boundary and greater than the highest boundary, respectively. The interval
148 boundaries of temperature and irradiance were specified to vary every 2 °C in the
149 range 22–30 °C and every 5 mol quanta m^{-2} d^{-1} in the range 5–40 mol quanta m^{-2} d^{-1},
150 respectively. The interval boundaries for nitrate, 0.1, 0.3, 0.5, and 1 μmol L^{-1}, were
151 uneven because the distribution of nitrate concentrations was highly right skewed (Fig.
152 S2). The mean relative abundance of each group and the standard error (SEM,
153 standard deviation divided by the square root of the number of data) were calculated
154 within each specified interval. Although information about realized niches that were
155 obtained via machine learning methods (Generalized Additive Models and Maximum
156 Entropy Models) based on raw data in the upper 150 m has already been described in
157 Xiao et al. (2018b), the present analysis was different in that the data interpolation
158 was based on mean values in the upper mixed layer and thus no complex statistical
159 methods were needed.

160 *2.3. Data reduction, ordination, and classification for a three-dimensional niche*
161 *scheme*

162 In order to create a three-dimensional niche scheme that was useful for
163 characterizing the dynamics of the phytoplankton communities, the samples were
164 divided into a series of bins on the basis of different intervals of temperature,

irradiance, and nitrate. The interval boundaries of each niche dimension were the same as the individual niches. These bins represented $\sum_1^5 C_5^i \times \sum_1^8 C_8^j \times \sum_1^4 C_4^k =$ 118,575 possible three-dimensional niche divisions, where the C_n^m are the number of combinations of *n* interval boundaries taken *m* at a time, and the summation is over the number of interval boundaries for temperature (5), irradiance (8), and nitrate (4). The calculations began with one interval boundary for each environmental parameter, and hence there was a minimum of $2^3 = 8$ possible niches and a maximum of $6 \times 9 \times 5 = 270$ possible niches. We defined niches for which we had fewer than 3 samples as empty niches and niches with at least 3 samples as realized niches. For each niche division, we removed the empty niches and carried out a one-way analysis of variance on the remaining niches in which we compared the normalized between-niche sum of squares (between-niche variance) to the normalized within-niche sum of squares (within-niche variance) for each of the nine phytoplankton groups. We concluded that the relative abundance of a phytoplankton group varied significantly between niches if the ratio of the between-niche variance to the within-niche variance (V_w) significantly exceeded 1.0 based on an *F* test. We considered that the division into niches was informative if the smallest *F* statistic ($F_{\min}$) among the 9 phytoplankton groups exceeded the critical value. The critical value of the *F* statistic was associated with a type I error rate (p) of 0.005 to ensure that the overall type I error rate was <0.05, i.e., $1 - (0.995)^9 = 0.044$.

For the initial case of 8 possible niches, the corresponding candidate boundaries

for temperature, irradiance, and nitrate generated $C_5^1 \times C_8^1 \times C_4^1 = 160$ possible combinations. We removed combinations for which the number of empty niches was more than 1. For the 51 remaining combinations, we determined the optimum combination of niche boundaries by varying the boundaries until F_{min} was a maximum. The computer program that determined the optimum niche boundaries of 8 possible niches is presented as 'R Program 1' in the Supplementary Information.

To determine whether further subdivision of the niches was informative, we calculated the within-niche sum of squares with and without one more niche division. We then calculated the statistic F' as follows:

$$F' = \frac{(S_{wa} - S_{wb})/(D_{wa} - D_{wb})}{S_{wb}/(D_{wb})} \quad (3)$$

where S_w is the within-niche sum of squares, b and a represent the realized niches with and without one more niche division, and D_{wb} and D_{wa} are the associated degrees of freedom. The additional niche division was judged to have significantly reduced the V_w if the p value associated with F' was <0.005 for the group that had the largest F statistic (F_{max}) among the 9 phytoplankton groups. We chose the combination of niche boundaries that produced the smallest p value. This process was repeated until no significant reduction of the V_w could be achieved by further subdivision of the niches (Table S1). Computer programs that obtained the statistical information of all subdivisions of the optimum niche division of 8 possible niches and determined the final optimum niche division are presented as 'R Program 2' and 'R Program 3',

206 respectively, in the Supplementary Information.

207 The realized niches of the last niche division were selected to create the final
208 three-dimensional niche scheme using a Canonical Correspondence Analysis (CCA)
209 and clustering analysis based on the mean relative abundance of each phytoplankton
210 group and mean values of the associated environmental factors within each niche. A
211 Monte Carlo permutation test was used to test the significance of the correlation
212 between each environmental factor and community composition, and the results
213 showed that all the three environmental factors passed this test ($p < 0.05$ for all cases).
214 The scores of the groups along the first two canonical axes of the CCA were used for
215 clustering analysis. Ward's minimum variance clustering was conducted based on the
216 Euclidean distances among the standardized values of the first two canonical axes.
217 The number of clusters was determined by a scree plot that showed the changes of the
218 within-clusters sum of squares (Fig. S4). The CCA was done using the '*cca*' function
219 of the R package 'vegan' (Borcard et al. 2011). The parameter 'scale' was set as
220 'TRUE' to standardize the environmental factors to zero mean and unit variance. The
221 function '*ordicluster*' in the R package 'vegan' was used to overlay a cluster
222 dendrogram onto the ordination diagram. All analyses were done using R version
223 3.4.4 (R Development Core Team 2018).

224 **3. Results**

225 *3.1. Individual niche schemes*

226 The phytoplankton communities displayed some clear patterns in response to
227 changes in each niche dimension (Fig. 1). With increasing temperature, the relative
228 abundances of *Prochlorococcus*, *Synechococcus*, haptophytes_6, and dinoflagellates
229 increased, whereas those of other groups decreased (Fig. 1a). The system changed
230 from communities dominated by haptophytes_8 and diatoms at low temperatures to
231 communities dominated by *Prochlorococcus* and *Synechococcus* at high temperatures
232 (Fig. 1a). With increasing irradiance, the relative abundance of *Synechococcus*
233 increased greatly, the relative abundances of haptophytes_6 and dinoflagellates
234 increased slightly, and the relative abundances of haptophytes_8, prasinophytes,
235 cryptophytes, and chlorophytes decreased (Figs. 1b). The relative abundance of
236 *Prochlorococcus* was a unimodal function of irradiance with a peak at roughly 10–20
237 mol quanta m^{-2} d^{-1}, whereas that of diatoms was a bimodal function of irradiance,
238 with peaks at roughly 0–5 and 30–40 mol quanta m^{-2} d^{-1} (Fig. 1b). With increasing
239 nitrate concentrations, the relative abundances of diatoms, haptophytes_8,
240 cryptophytes, and chlorophytes increased, whereas those of other groups decreased
241 (Fig. 1c). Most of the trends were nonlinear, and some were clearly not monotonic
242 (Fig. 1). The implication is that these niche dimensions may not act alone but instead
243 may interact.

244 *3.2. Three-dimensional niche scheme*

245 When two levels of each of the three niche dimensions were combined, the

246 boundaries of 26 °C, 20 mol quanta m^{-2} d^{-1}, and 0.3 μmol L^{-1} for temperature,
247 irradiance, and nitrate, respectively, resulted in a largest F_{min} of 5.83 ($p = 6.75\times10^{-6}$)
248 (Fig. 2a). These boundaries defined the optimum niche division of 8 possible niches.
249 If any of the niche intervals increased, the number of possible niches increased in
250 proportion to the number of intervals, but the proportion of empty niches also
251 increased (Fig. 2b). At the same time, the F_{min} decreased with increasing numbers of
252 possible niches (Fig. 2c). The implication is that the significance of the niche division
253 declined with increasing numbers of intervals. As a result, increasing the number of
254 niches increased the percentage of non-significant niche divisions in which the
255 relative abundances of all nine of the phytoplankton groups did not vary significantly
256 (Fig. 2c). For the significant niche divisions, the value of the smallest V_w initially
257 declined as the number of niches increased, but then became constant or increased
258 after the number of possible niches reached about 50 (Fig. 2d). Haptophytes_8 was
259 the group that resulted in the F_{max} for all niche divisions (Fig. S3), and this group was
260 abundant in our study area (Fig. 1). The largest number of possible niches that
261 significantly reduced the V_w of haptophytes_8 was 24 (Tables S1 and S2). The
262 corresponding optimum niche boundaries were 26 and 28 for temperature (°C), 5, 15,
263 and 20 for irradiance (mol quanta m^{-2} d^{-1}), and 0.3 for nitrate (μmol L^{-1}). This
264 division of niche space produced 15 realized niches (Tables S1 and S2). Although
265 these niches were divided according to statistics associated with haptophytes_8, the
266 percentages of the total variance of each of the other eight phytoplankton groups that

267 were accounted for by the 15 realized niches were quite high (76%–96%) (Table S3).
268 We used the mean values of the 15 realized niches (Table S2) to create a
269 three-dimensional niche scheme. No significant correlations were found between all
270 pairs of environmental factors based on their mean values ($p > 0.05$ for all cases).
271 The CCA revealed that the 15 niches explained 81% of the variance of the
272 phytoplankton communities, almost all of which was contributed by the first two
273 canonical axes (Fig. 3). The ordination diagram based on the first two canonical axes
274 created a clear niche classification scheme for the phytoplankton communities (Fig. 3).
275 The first canonical axis was contributed mainly by nitrate, and the second canonical
276 axis by temperature-related factors (temperature and irradiance). The scree plot
277 showed that there was an "elbow" at the three-cluster solution, the suggestion being
278 that clusters >3 did not have a substantial impact on the total within-cluster sum of
279 squares. The dendrogram of the nine phytoplankton groups also showed three major
280 branches. One branch was linked to the diatom group, which was assigned to the two
281 niches with high values of both irradiance and nitrate concentration. The other two
282 branches divided the other eight groups into a cold type and a warm type. The cold
283 type included haptopytes_8, prasinophytes, cryptophytes, and chlorophytes, which
284 were linked to the niches associated with low temperature and irradiance. The warm
285 type included *Prochlorococcus*, *Synechococcus*, dinoflagellates, and haptophytes_6,
286 which were related to the niches associated with high temperature and irradiance. The
287 cold type groups were first classified along irradiance, whereas the warm type groups

were first classified along nitrate. Among the warm type groups, *Synechococcus* was close to the niches with the highest irradiance level (20–45 mol quanta m^{-2} d^{-1}), whereas *Prochlorococcus* was mostly linked to the niches with intermediate irradiance (5–20 mol quanta m^{-2} d^{-1}) at temperatures higher than 26 °C and the niche with the highest irradiance level at lower temperatures. In addition, *Prochlorococcus* was more negatively correlated with nitrate than *Synechococcus* (Fig. 3). Because the number of samples in each niche varied from 5 to 277 (Table S2), we randomly picked five samples from those niches that had more than five samples to calculate the average. We then used those mean values to create a three-dimensional niche scheme. The randomization was repeated 10 times, and the resulting niche schemes were almost the same as in Fig. 3. One such example is presented in Fig. S5.

4. Discussion

4.1. Practical considerations limit the number of niches

We found that increasing the number of possible niches decreased the $F_{\min}$ and increased the fraction of non-significant niche divisions (Fig. 2c). In addition, the decreasing trend of the V_w of all nine phytoplankton groups stopped after the number of possible niches reached about 50 (Fig. 2d). These results reflect the fact that the need to increase niches decreased with increasing numbers of possible niches, and there was a maximum number of niches above which further subdivision of the niches did not significantly reduce the estimate of the V_w for all nine of the phytoplankton

groups. Increasing the number of possible niches is the analog of adding more terms to a polynomial function to describe a curvilinear function. Because there is invariably some noise in data, at some point adding more terms to the polynomial amounts to fitting noise as opposed to the underlying relationship (Laws 1997). Based on similar logic, too fine a division of niches may amount to fitting noise. The reason is that temperature, irradiance, and nitrate do not explain all of the variability of phytoplankton community composition, so further subdividing the niche dimension amounts to fitting variability that is probably explained by factors other than these three environmental variables. In the case of polynomial regression, there is a straightforward way to decide when the function is fitting noise. The strategy is to find the point when the F statistic is lower than the critical F value (Laws 1997). Similarly, we used an F statistic (F') on the basis of decreases in V_w to decide how many niches to create. Our procedure selected 15 realized niches that resulted from 24 possible niches that consisted of 3 temperature levels, 4 irradiance levels, and 2 nitrate levels as the last significant niche division (Table S1). Such a small number of niches suggests that there is a practical limit to the number of niches that can be used for groups of organisms in specific regions.

4.2. Simplified niche scheme meets the goal of Occam's Razor

Using the 15 realized niches, we created a three-dimensional niche classification scheme that related phytoplankton communities to the niches via CCA and clustering

328 analysis (Fig. 3). The CCA results revealed that the 15 niches accounted for 81% of
329 the variability of the phytoplankton community composition. Such a high percentage
330 of the variance accounted for was possible because the number of niches was small
331 and the community information was represented by only nine groups at the class level
332 rather than a much larger number of species. The simplification (i.e., reducing the
333 number) of niches decreased the between-niche sum of squares (S_b) that the CCA
334 explained, whereas the simplification of communities may have decreased the S_w that
335 the CCA ignored but would show up as S_b with more niches being created. A CCA
336 analysis using the 549 raw samples produced a figure (Fig. S6) with a shape similar to
337 Fig. 3, but the percentage of the variance explained was much lower, and it was not
338 easy to distinguish the niches of the phytoplankton groups. Our results suggest that
339 simplification of both niches and communities is key to developing a niche scheme
340 that is able to yield realistic estimates of how phytoplankton communities might
341 respond to the impact of climate change. This simplification is the goal of Occam's
342 Razor, which aims to make the analysis no more complicated than necessary, or
343 equivalently, keep the analysis as simple as possible (Baker 2007). The idea of
344 representing the phytoplankton communities in terms of a small number of groups
345 rather than a large number of species is a common practice in food web models (Laws
346 2008), ocean biogeochemical models (Hood et al. 2006), and trait-based approaches
347 (Litchman et al. 2007). There is evidence that emergent simplicity in the microbial
348 community assemblage at higher levels of organization is a generic property of large,

diverse systems (Goldford et al. 2017). There are also precedents for holding the number of habitats to single digits. For instance, Bala et al. (2005) have broken down climate zones into 7 categories to address the effect of climate on the distribution of vegetation. Manipulation experiments also tend to follow the principle of Occam's Razor and keep the number and levels of variables small (Burson et al. 2018, Lewandowska et al. 2014). Our analysis is therefore a useful guide for experiments aimed at discerning how phytoplankton communities will respond to climate change.

4.3. Synecological findings support known ecological theories

Our niche scheme separated two critical ecological systems from each other, the River-dominated Ocean Margin (RiOMar) and the Ocean-dominated Margin (OceMar) (Dai et al. 2013). These systems are characterized by the left side and the right side of the scheme, respectively (Fig. 3). Phytoplankton communities are regulated mainly by nitrate and irradiance in the RiOMar system and by temperature-related factors in the OceMar system (Fig. 3). The scheme has also revealed two types of groups in the OceMar system, a cold type and a warm type (Fig. 3). We found that the groups of the cold type were divided primarily by irradiance, whereas those of the warm type were divided primarily by nitrate (Fig. 3). These results are consistent with the general view that temperature influences plankton mainly by changing metabolic rates (related to the balance of photosynthesis and respiration) in cold waters and mainly by affecting nutrient supply in warm waters (Lewandowska et al. 2014). Because

369 temperature and nutrient supply are often negatively correlated in the open ocean
370 (Finkel et al. 2010), our results are also consistent with the theoretical resource
371 competition model for phytoplankton communities, which assumes that the species
372 interaction shifts from competition for light to competition for nutrients as nutrient
373 supplies decrease and vice versa (Huisman and Weissing 1995). These consistencies
374 indicate that our niche classification scheme is sufficiently general and may be
375 broadly applicable.

376 *4.4. Synecological findings challenge some views based on autecological studies*

377 Our niche scheme clearly assigned diatoms to the niches with both high nitrate
378 concentrations and high light intensity (Fig. 3). Culture studies have suggested that
379 diatoms are generally better adapted to low irradiances under high-nutrient and
380 strong-mixing conditions (Falkowski 1980). Our analysis does not support this
381 paradigm. The reason for this disagreement might be that our approach was
382 synecological rather than autecological. Our field database included the relative
383 abundances of a full range of sizes of phytoplankton at the class level. Synecology
384 considers that the competitive ability of a group depends not only on the physiological
385 response of the group itself but also on that of other groups (Walter and Hengeveld
386 2000). Under very low-light conditions, other groups, especially haptophytes_8, could
387 outcompete diatoms (Fig. 1c) at low temperatures, such as a well-mixed water column
388 in the winter (Schoemann et al. 2005). However, light-sufficient and nutrient-rich

389 environments in the SCS reflect the impact of the eutrophic and highly stratified Pearl
390 River freshwater plumes in the northern SCS during warm seasons, and under such
391 variable and co-limiting conditions diatoms tend to outperform other groups (Ning et
392 al. 2004). Similar results have been found in the East China Sea (Liu et al. 2016, Xiao
393 et al. 2018a) and in competition experiments using natural phytoplankton
394 communities as inocula (Burson et al. 2018). We therefore suggest that the results of
395 autecological studies of a limited number of species without consideration of
396 inter-species interactions can be misleading with respect to predictions of effects in
397 the real ocean.

398 Although photoinhibition of *Prochlorococcus* has been reported previously
399 (Chen et al. 2014, Flombaum et al. 2013, Six et al. 2007, Xie et al. 2018, Zinser et al.
400 2007), our niche scheme revealed that *Prochlorococcus* was linked to a high
401 irradiance niche at low temperatures but to intermediate irradiance niches at high
402 temperatures (Fig. 3). The implication is that the irradiance niche of *Prochlorococcus*
403 depends on temperature. All phytoplankton are adversely affected if the irradiance to
404 which they are exposed becomes too great (Litchman and Klausmeier 2008). This
405 effect is generally characterized as photoinhibition and is related to the production of
406 reactive oxygen species (Nishiyama et al. 2006). Because this study was of a
407 synecological rather than autecological nature, a decline of the relative abundance of a
408 group of phytoplankton at high irradiance could be related to photoinhibition, or it
409 could simply mean that other groups of phytoplankton were better able to exploit high

irradiances. To incorporate the effects of high irradiance in our synecological study, we used a model that has been used to describe photoinhibition in autecological research (Platt 1980, Xie et al. 2015), but with the caveat that the model is purely descriptive and is not meant to imply cause-and-effect. The model was formulated as follows:

$$P = a + P_m(1 - e^{-E\alpha/P_m})e^{-bE\alpha/P_m} \quad (4)$$

In Equation (4), P is the relative abundance of a phytoplankton group, and E is the explanatory variable irradiance. The parameter a is the intercept, and α is the initial slope of the P vs. E curve. P_m is the light-saturated relative abundance of the group in the absence of "photoinhibition", and b is a dimensionless "photoinhibition" parameter. The combination of $b\alpha/P_m$ reflects the strength of "photoinhibition".

We fitted the model at three temperature intervals, low (24–26 °C), medium (26–28 °C), and high (28–30 °C) (Fig. 4). The irradiance model provided further evidence that "photoinhibition" of *Prochlorococcus* existed at all temperatures (Fig. 4). This 'photoinhibition' may be due to the fact that *Synechococcus* did better than *Prochlorococcus* at high irradiance (Fig. S7). The "photoinhibition" at moderate and high temperatures was the same, but it was twice as high at those temperatures as at low temperatures, and the threshold at which light became inhibitory was lower at moderate and high temperatures (Fig. 4). These results indicate that the "photoinhibition" effect on *Prochlorococcus* is a saturation function of temperature. This saturation function very likely resulted from the fact that the relative abundances

of other groups such as *Synechococcus* and diatoms were lower at low temperatures than at higher temperatures (Fig. S7). This discovery suggests that, from a synecological standpoint, one cannot assume that the "photoinhibition" of *Prochlorococcus* is a fixed trait but should take temperature as an important covariate when predicting climate change effects.

4.5. Responses of phytoplankton communities to environmental changes

Our niche scheme provided an opportunity to make inferences about possible effects of environmental changes on phytoplankton communities. Global warming is expected to lead to increases of sea surface temperature, greater thermal stratification of the upper water column, and a reduction of nutrient inputs to the mixed layer from sub-nutricline waters (shallower mixed layers and less upwelling) in the coming century (Doney et al. 2012). There is also evidence that warming could bring more frequent and extreme rain events (Wentz et al. 2007), which would increase the impact of land runoff on coastal waters. Anthropogenic nutrient pollution would add to the eutrophication of coastal waters caused by these freshwater plumes (Anderson et al. 2002). Under such conditions, the cold type groups such as haptophytes_8, prasinophytes, cryptophytes, and chlorophytes would presumably be at a disadvantage because they were assigned to the low-temperature, low-irradiance niches (Fig. 3). The diatom group was linked to the high-nitrate and high-irradiance niches (Fig. 3). The impact on diatoms would therefore be mixed: they would benefit from higher

451 irradiance in nutrient-replete waters, such as most coastal regions, seasonally mixed
452 shelf seas, and eutrophic freshwater plumes, but they would be adversely affected by
453 the higher temperatures (fewer nutrients) in nutrient-limited waters such as the
454 seasonally stratified shelf seas and oligotrophic open ocean.

455 The warm type groups, including *Prochlorococcus*, *Synechococcus*,
456 dinoflagellates, and haptophytes_6, would benefit from sea-surface warming. This
457 would be especially true for *Prochlorococcus* and *Syenchococcus*. However, the
458 relative competitive ability of these two picophytoplankton would depend on the
459 nutrient status of their habitat. In mesotrophic environments such as stratified shelf
460 seas, mixed open oceans, and mesotrophic freshwater plumes, *Synechococcus* would
461 benefit more than *Prochlorococcus* because its irradiance and nitrate niches are higher
462 than those of *Prochlorococcus* (Fig. 3) and the effect of "photoinhibition" on
463 *Prochlorococcus* would be twice as great if the temperature increased by more than 2
464 °C (Fig. 4). This is very likely to happen by the year 2100 because at that time a
465 temperature rise of 2 °C compared to the pre-industrial era has been predicted by
466 scenarios of the Representative Concentration Pathways (RCP) 4.5–8.5 in most of the
467 ocean, especially in high latitudes of the northern hemisphere (Gattuso et al. 2015,
468 Stocker et al. 2013). In stratified oligotrophic waters, *Prochlorococcus* would have an
469 advantage over other groups because the negative effect of temperature on other
470 groups would be enhanced, but the "photoinhibition" effect on *Prochlorococcus*
471 would be the same (Fig. 4).

Changes of phytoplankton communities can have large impacts on aquatic ecosystems and global biogeochemical cycles (Litchman et al. 2007). Whether the observed results are unique for the SCS or are widespread among other marine ecosystems remains to be determined. Our analyses were based on a synthesis of a large-scale field database spanning more than 10 years rather than on a few cases. A caveat of our niche classification scheme is that the sample sizes varied greatly between niches. Although this did not change our results because we used only mean values, there is still a need to collect more field observations to expand the sample sizes. Another caveat is that our inferences on responses of phytoplankton communities to climate changes were based solely on a CCA analysis, which is qualitative and does not reveal causation. Controlled experiments are needed to test whether our results are reproducible. Also, we did not consider the other four niche dimensions proposed by Winemiller et al. (2015), including life history, trophic position, defense, and metabolism. These four dimensions may collectively be associated with ocean acidification (Gao et al. 2012), nutrient ratios (Klausmeier et al. 2004), grazing by zooplankton (Edwards and Richardson 2004, Lewandowska et al. 2014), and losses to viruses or pathogens (Burson et al. 2018). However, because the percent of the total variance accounted for by the 15 realized niches was 76–99% for all nine phytoplankton groups (Table S3), addition of more dimensions would be unlikely to greatly improve the explanatory capability of the niche classification scheme. Furthermore, our purpose was to identify the important and available niche

493 dimensions and try to keep things simple according to the principle of Occam's Razor.
494 If one other niche dimension is invoked, the number of niches will be immediately
495 doubled, and of course the number of niches becomes a geometric series as more
496 dimensions are added.

497 **5. Conclusions**

498 This study provided a novel approach for selecting optimum niche numbers and
499 niche boundaries to produce a simplified phytoplankton niche classification scheme
500 that characterizes the full size range of phytoplankton communities. The main
501 conclusions can be summarized as follows:

502 • There is a practical limit to how many niches the niche table contains for the
503 purpose of predicting the responses of phytoplankton communities to climate
504 changes.

505 • The simplified niche scheme supported general ecological theories, such as
506 physical and metabolic pathways of warming effects on plankton and
507 theoretical resource competition models for phytoplankton communities.

508 • The niche scheme also challenged some concepts based on autecological
509 studies on two phytoplankton groups, diatoms and *Prochlorococcus*, and
510 thereby enabled more informed predictions of their fates under future climate
511 change scenarios.

512

513

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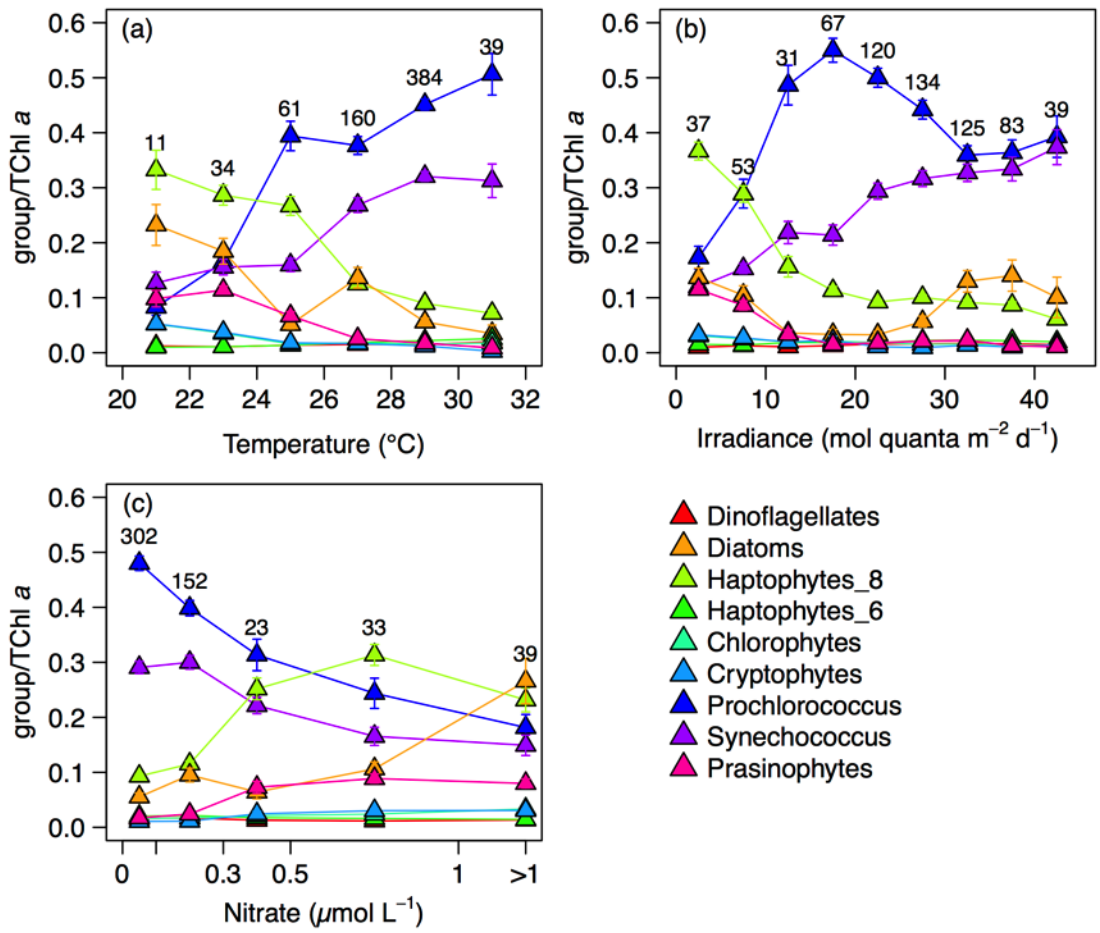


711

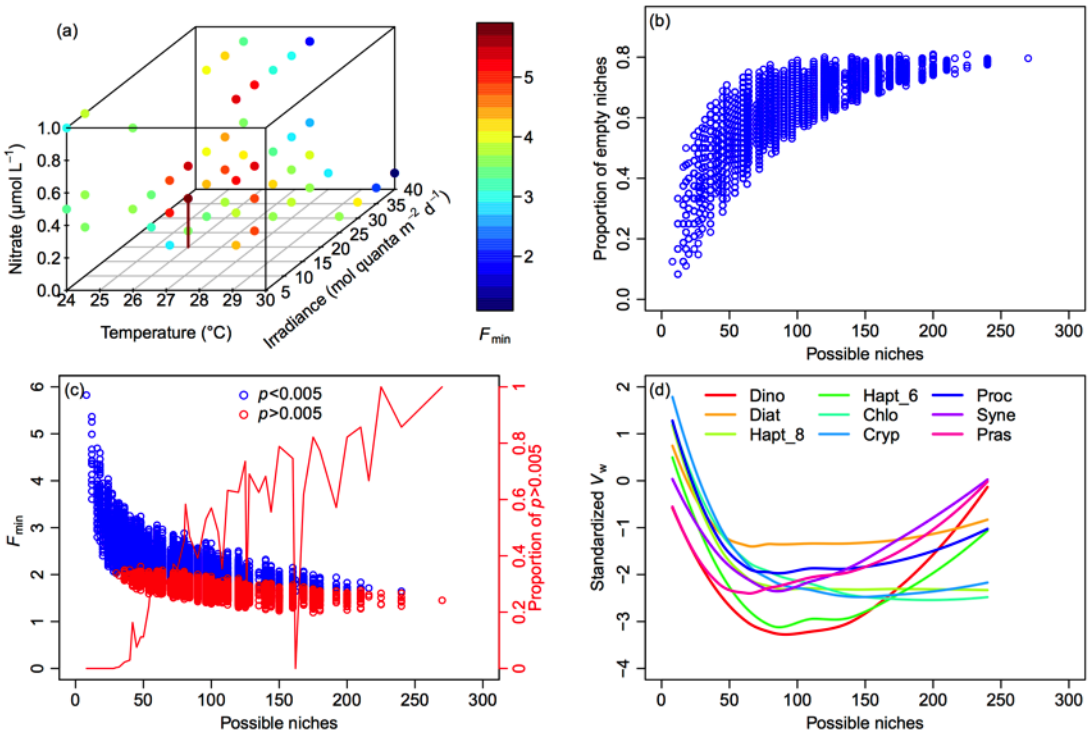
712 **Fig. 1** Relative abundances of phytoplankton groups as a function of individual niche

713 dimensions in the upper mixed layer. Error bars are the SEM. Digits above each bin

714 show sample sizes. The total number of samples was 689 for (**a**) and (**b**) and 549 for

715 (**c**).

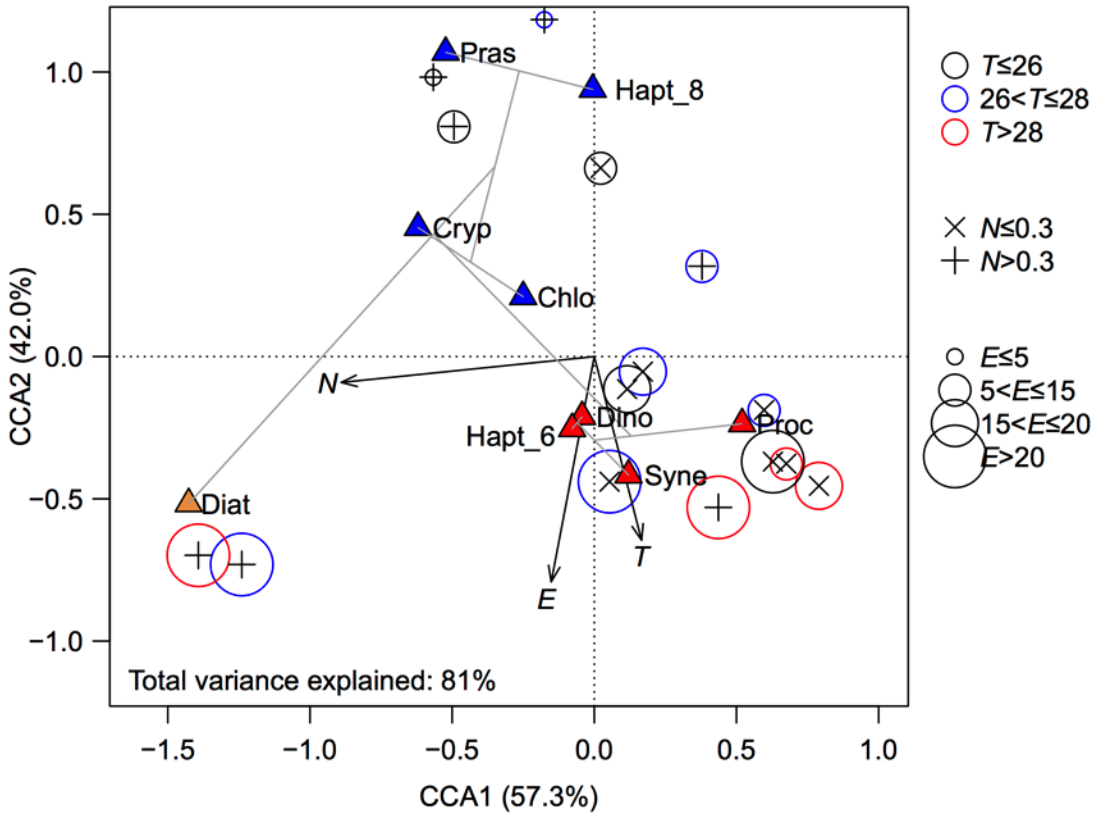
716



717

718 **Fig. 2** Statistical information for deciding where to draw the boundaries between
719 niches and how many niches to create. (**a**) The F_{min} resulted from 8 possible niches
720 versus niche boundaries; the optimum boundaries were marked in a dark red line; the
721 niche divisions with more than one empty niche were removed. (**b**) The proportion of
722 empty niches versus the numbers of all possible niches. (**c**) The F_{min} and the
723 proportion of non-significant niche divisions ($p > 0.005$) versus the numbers of all
724 possible niches. (**d**) Loess curves between the smallest standardized V_w (within-niche
725 variance) and the numbers of all possible niches; the niche divisions in which the
726 relative abundances of all of the nine phytoplankton groups did not vary significantly
727 (marked in red in (**c**)) were removed. Statistical information for drawing these figures
728 were obtained by 'R Program 1' (**a**) and 'R Program 2' (**b**–**d**) in the Supplementary
729 Information.

730



731

732 **Fig. 3** A three-dimensional niche classification scheme produced by CCA and
733 clustering analysis based on mean values of 15 niches. Every circle is a niche and
734 every triangle is a phytoplankton group. Sample sizes of the niches are presented in
735 Table S2. The dendrogram was overlaid by grey segments. Colored triangles showed
736 three clusters of phytoplankton groups determined by clustering analysis. *T*:
737 temperature (°C); *E*: irradiance (mol quanta m^{-2} d^{-1}); *N*: nitrate (μmol L^{-1}).

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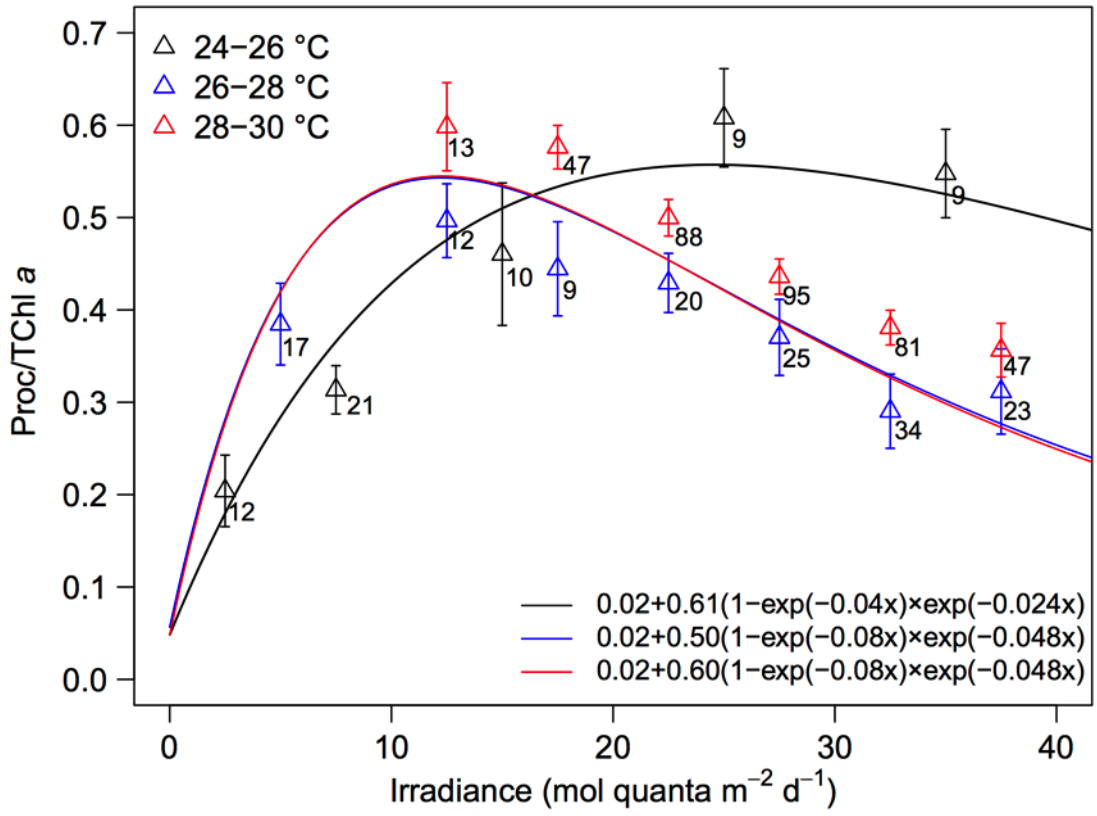

739

740 **Fig. 4** The relative abundance of *Prochlorococcus* as a function of irradiance at

741 different temperature intervals. Digits next to triangles show sample sizes. The

742 vertical axis is the mean and SEM of the relative abundance at each combined bin of

743 temperature and irradiance.

744